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Section II: Chapter 32

Accommodation Dynamics

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32.1 Introduction

Ocular accommodation describes the neuromuscular process which allows the eye to focus clearly objects located at distances from infinity to a near point determined by the amplitude of accommodation and is a reflex response which appears to occur instantaneously in pre-presbyopic individuals (Rosenfield et al., 2009). Objects continue to appear clear when attention is altered from one object to another even when a significant increase in ocular accommodation is required (Glasser, 2011). Increases in accommodation for near focusing are produced by an increase in the optical power of the crystalline lens, first identified by Thomas Young(1801). Young was able to identify through a series of elegant experiments that the radius of curvature of both surfaces of the crystalline lens decreased during accommodation, and the theory of decreased tension was subsequently developed by Helmholtz (1865) to describe the physical changes in the crystalline lens during accommodation (Helmholtz, 1856).

Until recently the techniques available for measurement of the accommodation response precluded the investigation of dynamic responses. The advent of continuously recording, infrared, objective optometers,

which did not interfere with experimental viewing conditions allowed the dynamics of the accommodation response to be investigated systematically across a range of controlled stimulus conditions (Collins, 1937; Heron and Winn, 1989). Collins' (1937) early pioneering work using an ingenious electronic refractometer was the forerunner of laboratory based infrared optometers and subsequently modern clinical autorefractors (Wood, 1987).

32.2 Control of the Accommodation Response

The accommodation response can be understood to have two primary functions; the ability to alter ocular power rapidly in response to a change in object or fixation distance, and the ability to maintain a steady level of focus at a chosen fixation distance[2], and the neuromuscular system of accommodation is ideally suited to these functions (Glasser, 2011). Rapid alterations in response occur reflexively and are known as step changes in accommodation due to the characteristic trace obtained when recording such responses continuously (Glasser, 2011; Heron and Winn, 1989). Perceptually there is no effect upon vision during a step response despite significant dioptric change in accommodation level (Schor et al., 1992), and the response acts in a reflex manner producing the required alterations in ocular power without any conscious input (Schor and Kotulak, 1986; Schor et al., 1992).

The second function of the accommodation system, which has important evolutionary consequences by allowing humans to work at close distances with fine tools, is the ability to maintain accurate steady-state focus at a fixed distance (Glasser, 2011). Again the steady-state response occurs without conscious control and the accommodation system makes continual, fine adjustments necessary to maintain clear focus, which can be can maintained for considerable periods of time (Glasser, 2011).

The primary stimulus to accommodation has received considerable attention over time. Maddox (1893) described the 4 classes of accommodation response as reflex, tonic, psychic and cross stimulation from vergence eye movements. The reflex response in Maddox' classification was taken to be the response to blur of the retinal image, while the psychic response represented mainly proximal stimulation arising from a knowledge of the spatiotopic relationship between the subject and the object being viewed (Schor et al., 1992).

Early experiments by Fincham (1951) and Allen (1955) using coincidence optometers showed that the accommodation response to blur stimuli with a magnitude of ~1.50D or less occurred in the correct direction 99% of the time, suggesting that not only was blur the primary stimulus to accommodation, but the accommodation error detection system had the ability to extract odd-error directional information from an even-error stimulus.

Neurological control of accommodation is via the autonomic system, primarily parasympathetic, arising from the Edinger-Westphal nucleus of the IIIrd cranial nerve (Glasser, 2011). There is a small (2% of nerve fibres) β-adrenergic input to the ciliary muscle arising from the superior cervical ganglion (Gilmartin, 1986). To understand the mechanisms of accommodation control and to characterize the response, a number of investigators have used modeling techniques from the engineering domain (Schor and Kotluk, 1986; Hung and Semmlow, 1980; Toates, 1970). Schor and Kotulak's (1986) dual mode systems control model described the components necessary to produce both dynamic step changes and steady-state responses in accommodation when blur is the primary stimulus for accommodation (Figure 1).

Insert figure 1 here

The model contains a phasic element with an integral controller to produce rapid step changes in accommodation response. The output of this controller is fed forward to an adaptive element with a slower time constant, which produces the ongoing output necessary to maintain a steady-state response at that level (Schor and Kotulak, 1986). A key component of all models was negative feedback of the response level, which was then subtracted from the required stimulus level in order to determine the need for further phasic response. The presence of negative feedback is essential in any feed-forward system to maintain response stability (Schor and Kotluk, 1986; Hung and Semmlow, 1980; Toates, 1970). Subtraction of negative feedback from the required stimulus level results in an accommodative error signal which must be greater than the system dead space (in this case the ocular depth of focus) in order to initiate a new response. With some minor alterations these models describe well the accommodation response to optical blur stimuli (Schor and Kotluk, 1986; Hung and Semmlow, 1980; Toates, 1970).

Difficulties arise in our understanding of the accommodation system when we consider the response to pure blur stimuli greater than ~1.50D. A number of early studies showed clearly that the accommodation response to pure blur stimuli of 2D or larger demonstrated even error behaviour, suggesting that the accommodation error detector could not a directional signal from the larger blur stimulus (Stark and Takahashi, 1965; Smithline, 1974). This inconsistency was addressed by recent studies demonstrating how potent perceived proximity was as a cue for the accommodation response (Schor et al., 1992; Rosenfield et al., 1991; Morrison et al., 2010). Consideration of the complementary but distinct operating ranges for the stimuli of blur and proximity strongly suggested that large accommodation

responses would be initiated by spatiotopic, proximal stimuli, until the accommodation response reduced the blur error signal to levels within the retinotopic blur stimulus range which could then refine the accuracy of the accommodation response to the optically required level (Schor et al., 1992). They developed a model based on that described previously which summarized this retinotopic/spatiotopic division of the accommodation response and how such a system would enable accurate accommodation responses to any change in object or fixation distance across the full range of the accommodation system (Schor et al., 1992).

32.3 Accommodation Step Responses

Empirical observation shows that the response time for accommodation begins to increase concurrently with decreases in the amplitude of accommodation response around the age of 45 years in Caucasian patients (Rosenfield et al., 2009; Glasser, 2011). This deterioration of the accommodation system leads to a functional inability to focus near distances which progresses until no useful accommodation response is found at around 60 years of age, and has been termed presbyopia (Rosenfield et al., 2009; Glasser, 2011). The majority of studies investigating dynamic accommodation responses have therefore been conducted on pre-presbyopic adults.

Campbell and Westheimer (1960) conducted a ground-breaking series of experiments to investigate the dynamic accommodation response using both step and sinusoidal changes in stimulus vergence. They used a newly constructed infrared optometer to measure continuously the accommodation response during an abrupt 2D change in stimulus vergence under monocular conditions (Figure 2).

Insert figure 2 here

They reported reaction times typically between 300–400ms with a maximum velocity of around 10Ds^{-1}. The average response time for far–to–near accommodation was 0.64s and for near–to–far accommodation, 0.56s. Therefore the total time for an accommodation response to a dynamic step stimulus of 2D was approximately 1s. However, they did report variability in responses between observers and viewing conditions (Campbell and Westheimer, 1960).

The dynamic accommodation response to abrupt changes in stimulus level has been evaluated comprehensively by a number of groups around the world following these initial experiments by Campbell and Westheimer (1960). A number of studies have shown that near–to–far accommodation has a longer response time than that found for far–to–near responses (Mordi and Ciuffreda, 1988; Heron and Winn, 1989; Heron et al., 2001; Seidel et al., 2003; Seidel et al, 2005), and continuous accommodation recordings show that the near–to–far response has a different pattern with a more gradual reduction in response compared to the abrupt increase found for far–to–near responses (Figure 3) (Campbell and Westheimer, 1960; Heron and Winn, 1989).

Insert figure 3 here

The majority of these studies have been conducted monocularly to avoid input from vergence eye movements via the crosslinks between the two systems described previously (Schor and Kotulak, 1986; Schor et al., 1992). When dynamic step responses of accommodation are measured binocularly, then reaction and response times have been shown to be the same as those found in monocular conditions (Seidel et al., 2005), with the responses

showing a high degree of symmetry between the two eyes (Figure 3) (Campbell and Westheimer, 1960; Heron and Winn, 1989). The addition of binocular vergence eye movements does provide the accommodation-vergence complex with an odd error signal in the form of binocular retinal image disparity which allows both systems to respond in the correct direction (Tyler, 1983). This interaction between the accommodation and vergence systems has been shown previously to be active primarily during the phasic element of the response (Schor and Kotulak, 1986), meaning that during the steady-state response there is a requirement for odd error modulation of retinal image blur in order to maintain accurate steady-state focus.

Abrupt step changes in accommodation show a temporal, dual mode pattern of response with an initial preprogrammed component, which generates a ballistic response not influenced by negative feedback of retinal image blur (Hung and Ciuffreda, 1988; Schor and Bharadwaj, 2006). Studies have shown that during this period of the step response the interposition of a further blur stimulus does not affect the completion of this preprogrammed component (Hung and Ciuffreda, 1988; Schor and Bharadwaj, 2006). Once the preprogrammed response is completed, the response level will be within the range of the retinotopic negative feedback control system, which then completes the response bringing it within the ocular depth of focus. This dual mode control of step responses of accommodation has been modeled using the same engineering tools as described previously (Hung and Ciuffreda, 1988; Schor and Bharadwaj, 2006)..

With accommodation responses taking up to 1s to complete for a large dioptric change, it is interesting to note that objects rarely appear blurred during an accommodation step response (Glasser, 2011), although there would be ample time for the sensory visual system to recognize and process this information (Wurtz, 2008). Saccadic suppression is a well

documented process which prevents the visual system from becoming perceptually aware of the motion of the images across the retina during a saccadic movement (Burr et al., 1994). For large saccadic movements this motion can reach speed of up to 500 deg/s Alhazmi et al., 2014). Saccadic suppression has been shown to increase thresholds primarily for the detection of low spatial frequency information (Burr et al., 1994). In contrast, the accommodation system detects and responds to image blur, which affects high spatial frequency information to a greater extent (Schor et al., 1992; Hung and Semmlow, 1980). Recent studies have demonstrated a suppression mechanism, which suppresses the sensory visual response to retinal image blur during abrupt step changes in accommodation response, by selective suppression of high spatial frequency content in the target (Mucke et al., 2008; Mucke et al., 2010).

32.4 Steady-State Response

An important characteristic of the accommodation response is the ability to maintain stable, clear focus upon an object of regard for relatively long periods of time (Rosenfield et al., 2009; Glasser, 2011). The accommodation system shows a characteristic pattern of accommodative lead for targets at a distance of ≥1m, and a lag of accommodation at for closer targets (Rosenfield et al., 2009; Glasser, 2011).

Intriguingly, when the steady-state accommodation response is measured continuously it demonstrates a continual variation in response level with an amplitude of ~0.5D and temporal frequencies up to ~5Hz (Campbell et al., 1959). This temporal instability in the steady-state accommodation response has attracted the interest of a number of investigators over the last 80 years since the first direct observation of these accommodative microfluctuations by Collins (1937). A number of investigations of steady-state accommodation dynamics suggest that rather than being an extraneous

characteristic of the steady-state accommodation response, microfluctuations could provide the odd error cue required to maintain an optimum accommodation response by providing subthreshold changes in retinal image contrast which could be detected by the sensory error detection mechanism (Winn and Gilmartin, 1992; Charman and Heron, 2015).

The first systematic investigation of the magnitude and temporal characteristics of the steady-state response concluded that microfluctations must play a role in sensory feedback (Campbell et al., 1959). They reported temporal frequencies up to 3Hz with dominant components occurring under 0.5Hz and between 1.3 and 2.2Hz (Figure 4).

Insert figure 4A here

Insert figure 4B here

A number of groups have confirmed the observation that the waveform of the microfluctuations exhibits temporal variations characterised by two dominant regions of activity: a low frequency component (LFC) typically broadband with frequencies up to 0.6Hz, and a high frequency component (HFC) typically narrowband and occurring in the range of frequencies between1.0Hz and 2.3Hz (Winn and Gilmartin, 1992; Charman and Heron, 2015). The microfluctuations typically occur with a root-mean-square (rms) magnitude of approximately 0.02-0.25D, which has been shown to be positively correlated with increases in the level of accommodation response (Figure 5) (Denieul, 1982; Kotulak and Schor, 1986a).

Insert figure 5 here

Functionally, microfluctuations offer a means by which an odd-error, directional cue can be elicited from the primary, even-error stimulus of retinal image blur (Schor et al., 1992). By monitoring variations in retinal image contrast and correlating these with the small variations in dioptric power resulting from the microfluctuations, the accommodation error detection mechanism can maintain an accurate steady-state accommodation response within the ocular depth-of-focus for a given stimulus (Kotulak and Schor, 1986b; Hung et al., 2002). Previous work suggests that this modulation of retinal image contrast by accommodation microfluctuations is available to the accommodation system (Ludlam et al., 1968; Win et al, 1989; Metlapally et al., 2014).

As described previously, when all cues other than blur are removed the initial accommodation response to large step stimuli (>2D) is even error in nature (Stark and Takahashi, 1965; Smithline, 1974). This suggests that the microfluctuations are unlikely to play a role in guiding the initial response as the magnitude of change is beyond the range for retinoptopic information (Schor et al., 1992). Consideration of the latency of accommodation step responses (300-400ms) also suggests that a frequency component of ~2.5-3.3Hz would be required to provide the required directional information (Hung et al., 1982). In contrast the presence of odd-error cues to the accommodation step response has been established for small (<1.5D) changes in the stimulus to accommodation where the accommodation response shows a directional accuracy of 99% (Fincham, 1951; Allen, 1955).

A number of studies have examined the contribution of the two dominant frequency components within the microfluctuations to the negative feedback control mechanism of the steady-state accommodation response (Winn et al., 1990a and b; Gray et al., 1993a and b; Day et al., 2006; Day et al.,

2009). The source of the HFCs was of particular interest as their characteristics did not appear to be related to changes in stimulus parameters suggesting they may simply represent ‘plant noise’ derived from the mechanical and elastic properties of the crystalline lens and its support structures (Winn et al., 1990a and b; Winn and Gilmartin, 1992; Charman and Heron, 2015). Studies showed that while there is very little intra-subject variation in the peak frequency of the HFC, it was evident that there was significant inter-subject variation (Campbell et al., 1959; Winn et al., 1990a and b). The significant inter-subject variability led to consideration of the relationship between the HFC and other physiological systems which create rhythmic intraocular variation. Simultaneous measurements of ocular accommodation and systemic arterial pulse on 20 subjects demonstrated that the location of the HFC peak frequency was significantly correlated with arterial pulse frequency (Figure 6) (Winn et al., 1990a).

Insert figure 6 here

Subsequent studies revealed that the magnitude of the LFCs alters with changes in stimulus parameters in a manner which suggests they play a role in accommodation control (Campbell et al, 1959; Gray et al., 1993a and b; Day et al., 2006; Day et al., 2009). Reductions in pupil size are known to increase the ocular depth-of-focus (Campbell, 1957; Charman and Whitefoot, 1977; Atchison et al., 1997) with increases in the magnitude of the microfluctuations reported (Campbell et al, 1959; Gray et al., 1993a and b; Day et al., 2006; Day et al., 2009). Campbell et al. (1959) in their original paper showed that microfluctuations were larger through a 1 mm pupil compared to a 7 mm pupil (Figure 4 A,B.)

A systematic study of the relationship between pupil diameter and accommodation microflutuations was conducted with the stimulus placed at the subjects' tonic position to ensure that the mean accommodation response level remained constant throughout the study (Gray et al., 1993a). This was an important design feature of the study as it is known that accommodation microfluctuations are larger at higher levels of accommodation response (Denieul, 1982; Kotulak and Schor, 1986a). For pupil diameters >2 mm the fluctuations remained approximately constant with a rms magnitude of ~0.20D. A significant increase in the rms magnitude to ~0.31D was observed for pupil sizes ≤2mm, and these changes were found to be due primarily to an increase in the LFC (Figure 7) (Gray et al., 1993a).

Insert figure 7 here

Power spectrum analysis for a typical observer highlighted the increase in magnitude of the LFC for smaller pupil sizes while the HFC remains fairly constant in magnitude and frequency (Figure 8) (Gray et al., 1993a). The power of the LFC is approximately constant (0.05 D^2/Hz) for pupil sizes above 2mm but increases to 0.12 D^2/Hz for the 2 mm pupil, 0.13D^2/Hz for the 1 mm pupil and 0.22 D^2/Hz for the 0.5 mm pupil. Clearly the pupil diameters producing increases in the microfluctuations correspond with those that produce substantial increases in the ocular depth-of-focus (Gray et al., 1993a). The increase in magnitude of the microfluctuations has the potential to provide the accommodation error detector with consistent feedback as the size of the depth-of-focus increases.

Insert figure 8 here

It has been proposed that the presence of an inherent accommodative ‘lag’ or ‘lead’ (steady-state error) would enhance the effectiveness of microfluctuations (Charmand and Tucker, 1978) as it is known that the sensitivity to blur is increased when the retinal image is slightly defocused (Campbell et al., 1958). A computer simulation of an accommodative feedback control system identified the frequency of oscillation permissible in the response before the loop becomes unstable to be 0.45Hz which is consistent with a typical LFC (Hung et al., 1982). Opening the accommodation loop causes the response to regress to a tonic position (Gilmartin and Hogan, 1985) with large drifts in accommodative level occurring at low frequencies (Westheimer, 1957; Alpern, 1958; Baker et al., 1983; Gray et al., 1993b).

The overall profile of accommodative microfluctuations was thought to be the result of a combination of both neurological control and localised plant noise (Winn and Gilmartin, 1992; Charman and Heron, 2015). The HFC is not under direct neurological control but may still be utilised as part of the overall waveform in conjunction with the LFC by the accommodation error detector (Winn and Gilmartin, 1992; Charman and Heron, 2015). A functional role for the microfluctuations as an error-detector is probably related to the maintenance of focus on a stationary stimulus, as the neurologically controlled component is too slow to provide the necessary information to optimise the response to rapid step changes in stimulus vergence (Winn and Gilmartin, 1992; Gray et al., 1993a; Charman and Heron, 2015).

32.5 Detectability of Accommodation Microfluctuations

The microfluctuations introduce a blur stimulus which is smaller than the ocular depth-of-focus hence below the perceptual blur threshold, yet it is apparently of sufficient magnitude to provide the required odd-error

signal to the accommodation control system allowing maintenance of the steady-state response via negative feedback of retinal image blur (Schor et al., 1992). A model was described to explain how the accommodation error detector could extract the required information from sub-perceptual threshold stimuli (Kotulak and Schor, 1986b). Although the model was originally conceived using the high frequency (2Hz) component of the fluctuations it is equally applicable to any frequency of oscillation including those found within the LFC range (Gray et al., 1993a). Magnitude and directional information can be determined from sub-perceptual stimuli by calculating and comparing the first derivatives of temporal changes in retinal image contrast and temporal changes in ocular lens power (Kotulak and Schor, 1986b). Directional information is extracted by comparing the signs of the first derivatives of these two time functions; an over-accommodated eye will have the lens power function out of phase with the retinal contrast function; an under-accommodated eye will have these two functions in-phase (Kotulak and Schor, 1986b). The retinal image contrast is directly related to the instantaneous focus error present hence magnitude information can be extracted from the model by direct comparison of the two first derivatives (Kotulak and Schor, 1986b).

As stated previously low frequency drifts in the accommodation response are found when the system is placed under open-loop conditions (Westheimer, 1957; Alpern, 1958; Baker et al., 1983; Gray et al., 1993b). The slope of the accommodation stimulus/response curve decreases when the luminance of the target is reduced (Johnson, 1976), and reducing stimulus luminance has been shown to result in an increase in the magnitude of the microfluctuations and the magnitude of the LFCs in the waveform (Gray et al., 1993b). The magnitude of accommodation microfluctuations was constant for target luminances >0.010cdm^{-2} but increased and became more variable

for luminances ≤0.010 cdm^{-2}. The increase in magnitude of the fluctuations was attributable to changes in the LFC (Figure 9) (Gray et al., 1993b).

Insert figure 9 here

Reduction in stimulus luminance does not alter the stimulus contrast per se but causes the higher spatial frequency content within the target to fall below threshold producing a shallower contrast gradient in the cortical image, and consequently increasing the ocular depth-of-focus (Day et al, 2009). Day et al, (2009) showed that the contrast gradient and alterations in depth-of-focus resulting from reductions in target luminance remain relatively constant until the luminance is reduced to 0.002cdm^{-2}, which corresponds to the levels of luminance found to produce increases in the magnitude of the microfluctuations (Gray et al., 1993b).

The relationship between ocular depth-of-focus and accommodation microfluctuations has been used as the basis for investigation of differences between refractive groups. Several studies have reported that late-onset myopes (LOM: onset after the age of 15 years) demonstrate a larger depth-of-focus than emmetropes (Rosenfield and Abraham-Cohen, 1999; Vasudevan et al., 2006). Significantly larger microfluctuations have been reported in LOM compared to emmetropes suggesting that the larger depth-of-focus found in LOM leads to a higher threshold for retinal image blur (Seidel et al., 2003; Seidel et al., 2005; Day et al., 2006; Day et al., 2009).

32.6 Age-Related Changes in Accommodation Response

The ability to accommodate diminishes with increasing age resulting in the need for spectacles to read in patients over the age of 45 years, and the

underlying decline in the amplitude of accommodation with age has been well documented (Duane, 1912). There is a lack of consensus regarding the exact anatomical and physiological changes that underlie the onset of presbyopia (Kasthurirangan and Glasser, 2006) although regardless of the mechanism, presbyopia affects 100% of the population (Weale, 2003).

Although the decrease in amplitude with increasing age is well established, there has been less work on the age related changes in dynamics of the accommodation response. Measuring dynamic accommodation requires intrusive conditions for subjects including a head restraint and often the use of a dental bite to control head position (Winn and Gilmartin, 1992; Winn et al., 1990b). The calibration procedures are time consuming and repeated trials under these conditions can be challenging (Pugh and Winn, 1988). This has inevitably led to the use of small sample sizes, resulting in studies with equivocal results. This is especially important when looking for subtle age-related changes in the response, as significant inter-individual variation in accommodation response characteristics is known to occur (Charman and Tucker, 1978; Mordi and Ciuffreda, 2004).

Kasthurirangan and Glasser (2005) attempted to resolve this lack of consensus by conducting a study of accommodation dynamics in a large group (n=66) of subjects between the ages of 14 and 45 years. The experiment used a number of accommodation stimulus amplitudes over repeated trials, allowing a comprehensive analysis of data across the age range. They were able to confirm a linear decrease in accommodative amplitude with increasing age at a rate of 0.26D per year when measured objectively, and 0.35D per year for subject observations although significant inter-individual variability was apparent. Extrapolation of the data showed that

any functional accommodation response was completely lost at 50 years of age.

Measurement of accommodation step responses showed no differences in response latency with increasing age (Kasthurirangan et al., 2003). Time constants for accommodation step responses are known to increase linearly with increasing stimulus amplitude and this relationship was shown to increase with increasing age at a rate of 0.01s/D/year (Kasthurirangan et al., 2003). Interestingly this relationship occurred only for far to near responses and no systematic change in the relationship between time constants and response amplitude could be found for far to near responses (Kasthurirangan and Glasser, 2006; Kasthurirangan et al., 2003).

The amplitude of accommodation has an impact on response dynamics with the saturation level reducing with increasing age (Mordi and Ciuffreda, 2004). Saturation of the peak velocity occurs at lower response amplitudes with increasing age (Kasthurirangan et al., 2003). By evaluating responses well within the total amplitude it is possible to get a clearer view of age-related changes, and peak velocity was shown to be invariant with increasing response amplitude in older subjects but increases with response amplitude in younger subjects (Kasthurirangan and Glasser, 2006).

There appears to be a general consensus that the speed of the accommodation response declines with increasing age (Mordi and Ciuffreda, 2004; Kasthurirangan and Glasser, 2006; Kasthurirangan et al., 2003). However, the effect of increasing age on disaccommodation remains equivocal (Kasthurirangan and Glasser, 2006; Kasthurirangan et al., 2003). There have been several studies that report that disaccommodation does not change with age (Heron et al., 1999; Heron et al., 2001; Mordi and Ciuffreda, 2004; Kasthurirangan and Glasser, 2006). Other studies have

suggested a reduction in response dynamics (Scaeffel et al., 1993) although this finding may be the result of not adjusting for reduced response amplitudes in older subjects.

32.7 Conclusion

The accommodation response is a complex neuromuscular system that incorporates complex sensory processing and neurological control mechanisms into an effective sensorimotor reflex. While many aspects of the accommodation response and it's control are established it remains a useful probe for investigating aspects of the sensory visual system. The changes that occur in the accommodation response as a result of presbyopia are as yet not fully elucidated and require further investigation, and it is clear that the role of accommodation in the onset and progression of myopia is an area of considerable interest currently.

32.8 References

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Figure Legends

Figure 1

Schor and Kotulak (1986) system model representation of accommodation and vergence control and the interactions between the systems. The key elements are negative feedback subtracted from the desired stimulus level to produce an error signal. If the error signal is greater than the system dead space (for accommodation this would be ocular depth of focus) then a phasic response is initiated to shift the response level. Upon achieving this response level if fixation is sustained the output from the adaptive control element will increase to maintain the response. Note that the crosslink interaction between accommodation and vergence occurs after the phasic component but prior to the adaptive control output. For further description see Schor and Kotulak (1986). Reprinted with permission.

Figure 2

Record of accommodation responses to a 2D step stimulus and return to zero level of accommodation (subject F.W.C.). Allowance should be made for the arc of the pen. Top line, accommodation (length of horizontal line, 1 sec; height of arc, 1D): upward movement represents far-to-near accommodation. Bottom line, stimulus signal, same scale. This record is an example of single-sweep accommodation responses (after Campbell and Westheimer, 1960). Reprinted with permission.

Figure 3

A typical binocular accommodation response to a step change in target distance. The lower trace indicates the change in target vergence. The near-to-far response gradually approaches its final level in comparison with the far-to-near response (After Heron and Winn, 1989). Reprinted with permission.

Figure 4

A. Accommodation record of subject J.G.R. under normal viewing conditions with a 7mm pupil (upper) and with a 1mm effective entrance pupil of the eye (lower). The records have the same average accommodation level.

B. Frequency spectra of the two records shown in Fig.4A (linear ordinates).

(After Campbell, Robson and Westheimer, 1959). Reprinted with permission.

Figure 5

Records of accommodation microfluctuations as a function of target vergence (V). Observer M.B. (After Denieul, 1982). Reprinted with permission.

Figure 6

Correlation between arterial pulse frequency and high-frequency component for group data (n=20: $r = 0.99$, $P<0.001$). The regression line is $y = 0.0604 + 0.9516x$. After Winn et al. (1990). Reprinted with permission.

Figure 7

Accommodation traces for one observer (subject NS) for each artificial pupil diameter. Each trace is of 10s duration and has been smoothed to 1OHz. Note the high incidence of low frequency components which can be identified for the smallest pupil diameters (0.5 and l.Omm) and which decreases for the larger pupil diameters. The incidence of high frequency components is approximately the same for all artificial pupil diameters. (Gray et al., 1993a). Reprinted with permission.

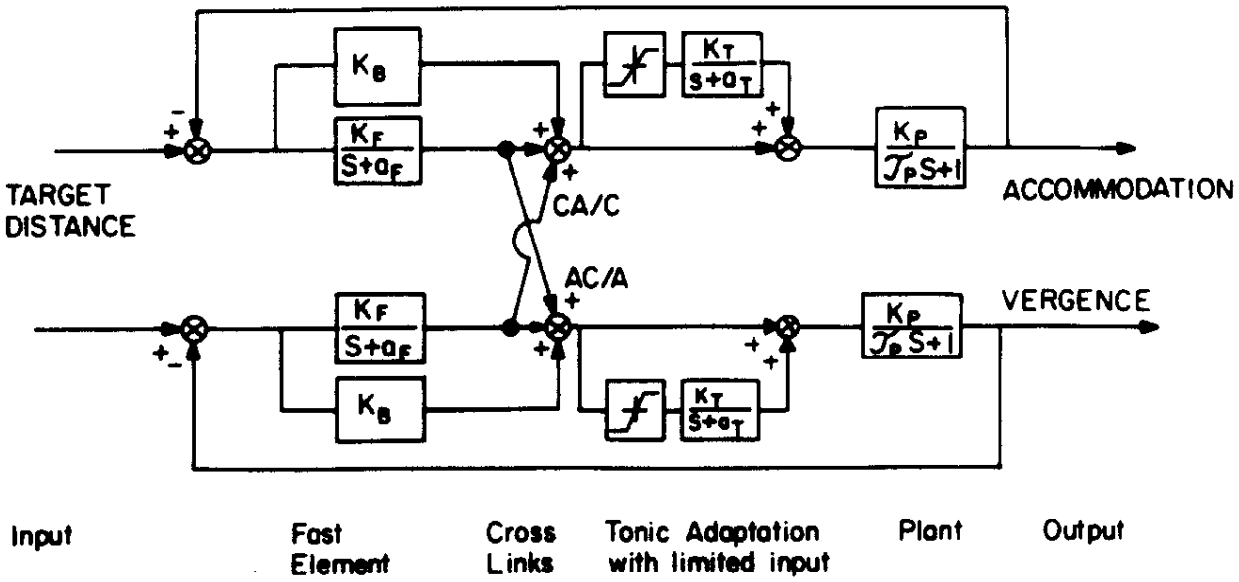
Figure 8

Mean power in the low frequency (LFC) and high frequency components (HFC) of the microfluctuations as a function of pupil diameter for the three subjects. Each point represents the mean of 15 power spectra and is calculated for three frequency bins. For further details see Gray et al. (1993a). Reprinted with permission.

Figure 9

Mean power in the low-frequency (open circles) and high-frequen components (closed circles) as a function of target luminance for three subjects. Each point represents the mean of 15 power spectra and is calculated for three frequency bins; error bars represent ±1SD. After Gray et al. (1993b). Reprinted with permission.

Figure 1



Input | Fast Element | Cross Links | Tonic Adaptation with limited input | Plant | Output

Figure 2

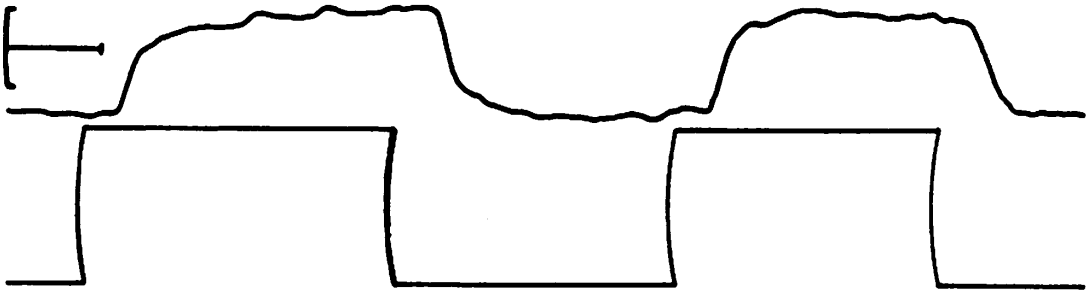


Figure 3

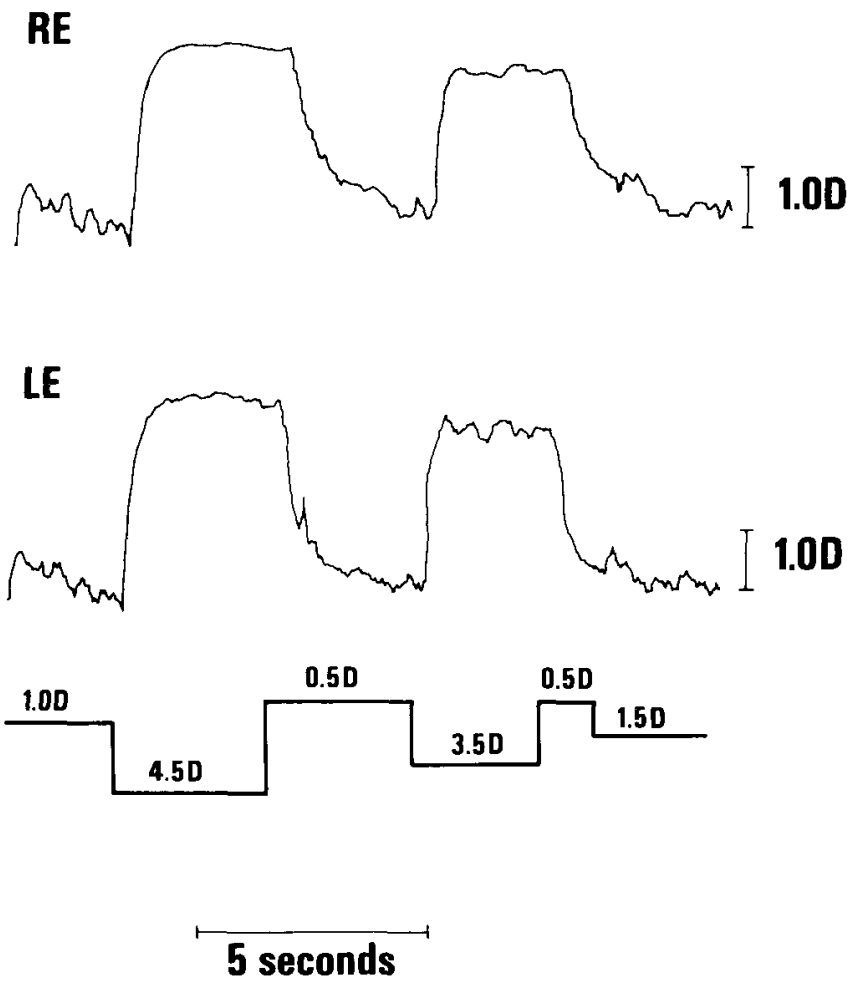


Figure 4A

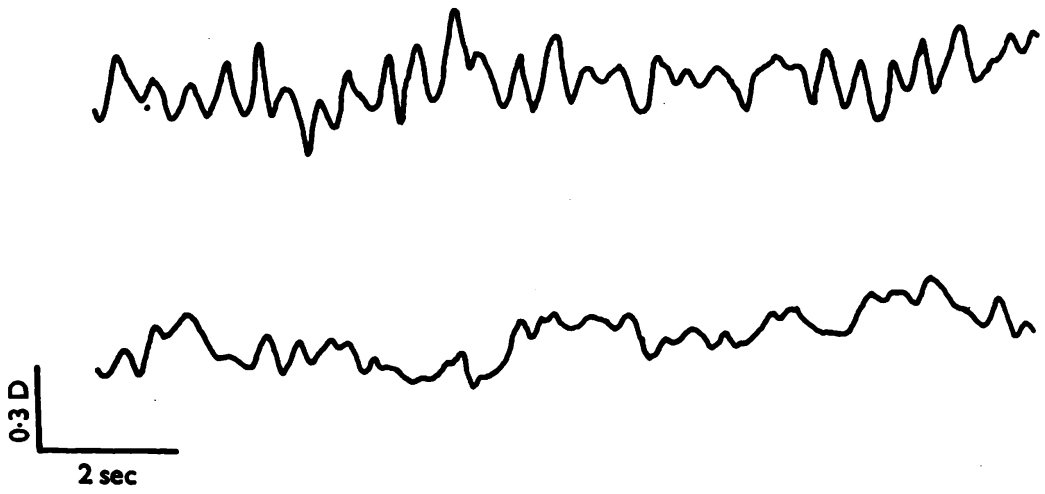


Figure 4B

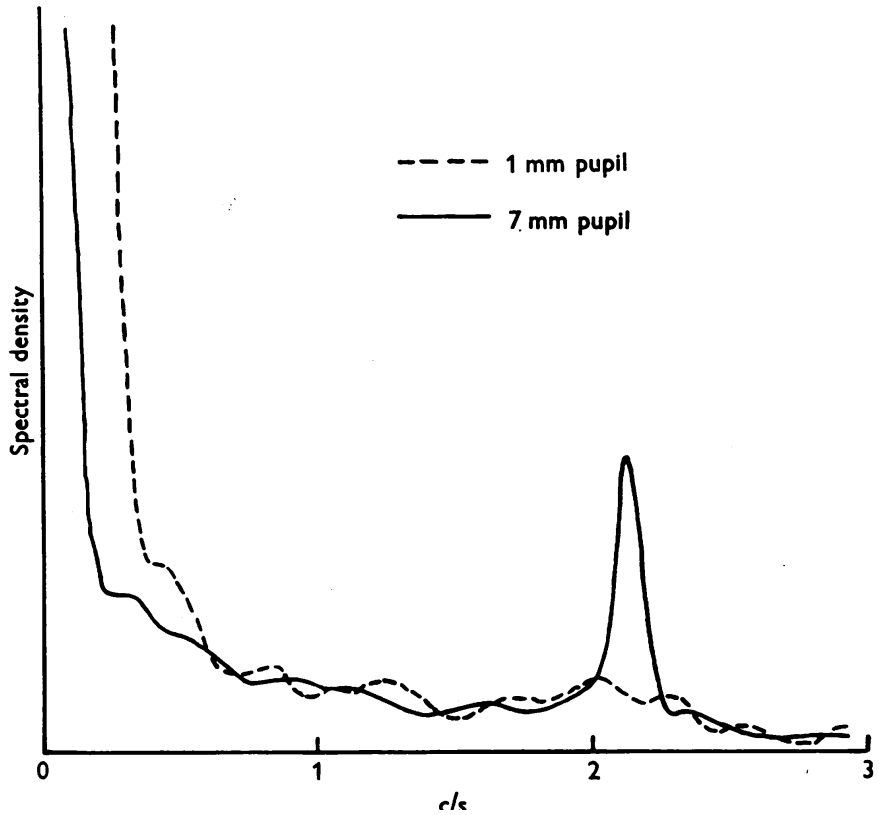


Figure 5

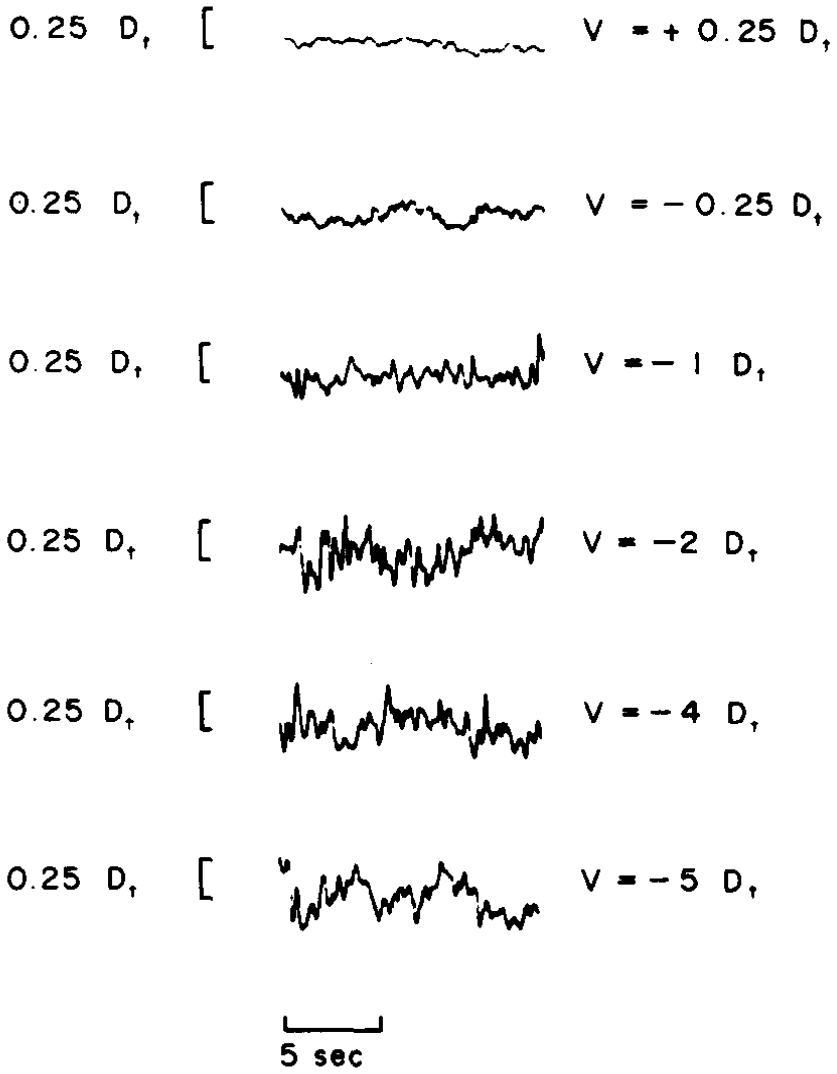

0.25 D,
V = + 0.25 D,
0.25 D,
V = − 0.25 D,
0.25 D,
V = − 1 D,
0.25 D,
V = −2 D,
0.25 D,
V = −4 D,
0.25 D,
V = −5 D,
5 sec

Figure 6

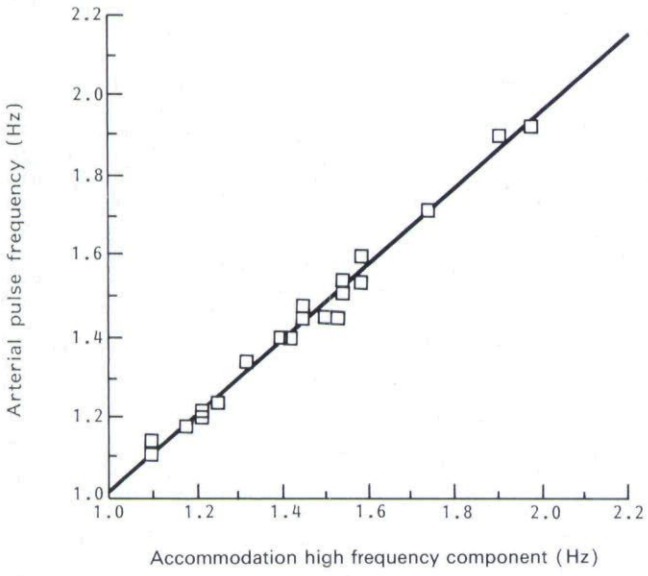

Arterial pulse frequency (Hz)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
1.0
1.2
1.4
1.6
1.8
2.0
2.2
Accommodation high frequency component (Hz)

Figure 7

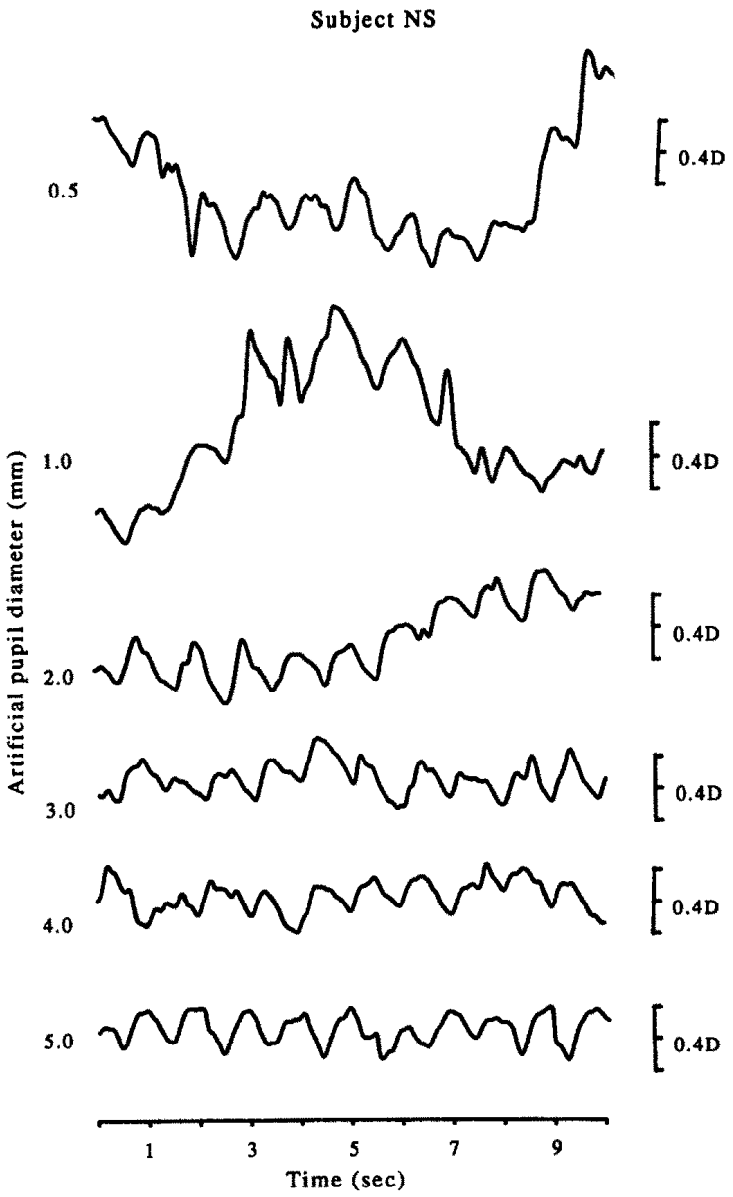

Subject NS
Artificial pupil diameter (mm)
0.5
1.0
2.0
3.0
4.0
5.0
0.4D
0.4D
0.4D
0.4D
0.4D
0.4D
1
3
5
7
9
Time (sec)

Figure 8

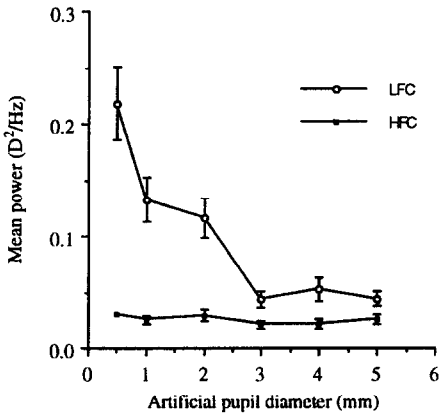
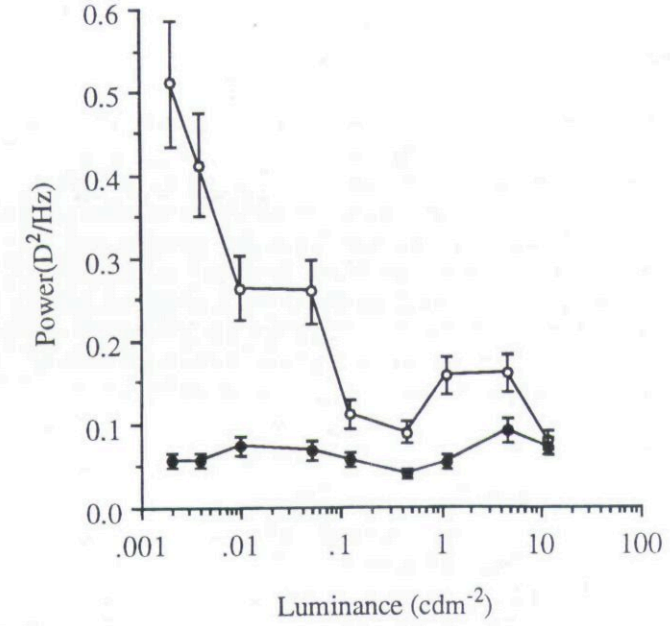

0.3
0.2
0.1
0.0
Mean power (D²/Hz)
LFC
HFC
0
1
2
3
4
5
6
Artificial pupil diameter (mm)

Figure 9



Index